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SHORT COMMUNICATION

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Behavioural responses of peach potato aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae), to entomopathogenic fungi infected conspecifics

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Abstract

1. Entomopathogenic fungi (EPF) can suppress aphid populations through biological control, but whether EPF-associated volatile cues influence aphid behaviour remains poorly understood. We investigated the olfactory response of apterous *Myzus persicae* to *Beauveria bassiana* and to conspecifics infected with *B. bassiana*.
2. Aphid responses were assessed using four-arm olfactometer assays. In the first assay, aphids were exposed to *B. bassiana*-colonised agar, sterile agar and two blank-air controls. In the second, aphids were exposed to odours from EPF-infected conspecifics, healthy conspecifics, an agar control and a blank-air control. Time spent within each odour field was converted to compositional proportions and analysed following centred log-ratio transformation.
3. Aphids showed no detectable olfactory response to *B. bassiana*-colonised agar alone. In contrast, aphids responded positively to odours associated with infected conspecifics, spending significantly more time in this odour field than in those containing healthy aphids, agar or blank air.
4. These findings demonstrate that the behavioural response of *M. persicae* to EPF-associated cues is context dependent, with cues generated during host infection appearing more salient than fungal odours presented in isolation.
5. The results extend our understanding of pathogen-mediated chemical communication in aphids and suggest that EPF infection may influence host–pathogen interactions and potentially pathogen transmission in ways that are not predicted by repellency-based models alone.

KEYWORDS
Beauveria bassiana, biological control, chemical ecology, olfactometer, volatile organic compounds

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INTRODUCTION

Peach potato aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae), is a globally important and highly polyphagous pest that damages crops directly through feeding and indirectly through the transmission of numerous plant viruses (Ali et al., 2023). The importance of this species as a pest reflects not only rapid population increase, but its wide host range, ability to assess habitat quality and respond rapidly to cues within chemically complex environments (Ali et al., 2023; Pickett et al., 1992; Webster, 2012). In aphids, olfaction underpins orientation to host- and non-host-derived volatiles, responses to conspecific cues and the regulation of settling, dispersal and escape behaviours; semiochemical perception is therefore central to both aphid ecology and aphid management (Pickett et al., 1992).

Entomopathogenic fungi (EPF) are among the most important microbial natural enemies of insects and have long been studied as biological control agents because they can cause increased pest mortality while posing relatively little risk to non-target organisms and the wider environment compared to conventional synthetic chemical insecticides (Butt et al., 2016; Shah & Pell, 2003). In aphid systems, EPFs such as *Beauveria bassiana* (Bals.-Criv.) Vuill., 1912, and *Metarhizium anisopliae* (Metschn.) Sorokin, 1883, can infect hosts directly, with some isolates also able to colonise plants endophytically, thereby influencing aphid survival, reproduction, feeding behaviour and, potentially, plant virus epidemiology (Fingu-Mabola et al., 2021; Wilberts et al., 2022). A growing body of evidence shows that insects can detect EPFs prior to physical contact, although the direction of the response is not consistent across systems. Avoidance of EPF-associated substrates, cadavers and habitats has been documented in several taxa, supporting the view that fungal cues can signal infection risk (Baverstock et al., 2010; Mburu et al., 2009; Meyling & Pell, 2006). However, fungal odours are not invariably negative. In *M. persicae*, positive responses to volatiles emitted by *B. bassiana* mycelia and conidia have recently been reported, challenging the assumption that EPF cues are necessarily aversive and suggesting instead that fungal volatile blends may function as context-dependent semiochemicals (Geedi et al., 2023). More broadly, EPFs produce complex and dynamic blends of volatile organic compounds whose composition varies with fungal species, strain, substrate and growth stage, all of which may influence how insects interpret those odours (Bojke et al., 2018; Holighaus & Rohlfs, 2016; Naundrup et al., 2022).

Less is known about whether healthy aphids respond to odours emitted by infected conspecifics. This distinction is important because infection may alter the chemical phenotype of the host itself rather than simply superimpose a fungal odour. Pathogens are increasingly recognised as modifiers of insect chemical communication, affecting pheromone signalling, volatile emissions and host behaviour in ways that can influence interactions between hosts and transmission dynamics (Moyano et al., 2023; Roy et al., 1999; Zhang et al., 2024). In aphids, this question is especially relevant because the alarm pheromone system, relying on (*E*)-β-farnesene, mediates rapid escape responses and shapes interactions among conspecifics and natural enemies (Vandermoten et al., 2012; Zhang et al., 2017). Earlier studies indicate that fungal infection can alter aphid alarm responses and feeding behaviours, raising the possibility that infected individuals emit cues that are detectable to healthy conspecifics (Baverstock et al., 2005; Roy et al., 1999, 2005). Against this background, a key unresolved question is whether healthy *M. persicae* respond to infected conspecifics in the same manner as they respond to the fungus alone. Addressing this gap is important for both fundamental chemical ecology and applied biological control as attraction to infected individuals could increase encounter rates and facilitate horizontal transmission, whereas avoidance could reduce secondary spread and alter the realised efficacy of EPF-based control. Here, we used four-arm olfactometer assays to compare the behavioural responses of apterous *M. persicae* to *B. bassiana* presented on agar with their responses to conspecific aphids infected with *B. bassiana*. We tested whether aphids exhibit a positive or negative behavioural response to each odour context and whether responses differ between fungal odours presented in isolation and those associated with infected hosts.

MATERIALS AND METHODS

Insects and entomopathogenic fungi

A colony of *Myzus persicae* Sulzer (Hemiptera: Aphididae) was maintained at Harper Adams University in a controlled-environment room at 18 ± 1°C and 60 ± 5% RH under a 16:8 h L:D photoperiod (Fitotron, Weiss Technik UK limited, Loughborough, UK) on seven-day old Pak choi (*Brassica rapa* subsp. *chinensis cv*. Hanakan) plants. Aphids used in the experiments comprised standardised cohorts of apterous adults with no prior exposure to the test treatments. Standardised cohorts were generated by transferring adults from the stock colony onto clean Pak choi plants and allowed to larviposit for 24 h, after which they were removed, leaving only first-instar nymphs. Nymphs were maintained under the same conditions as the stock colony and monitored daily until they reached adulthood, which was after approximately 7–8 days. Newly moulted adults were collected for use in experiments.

Beauveria bassiana (Bals.-Criv.) Vuill. strain ATCC 74040 was obtained from the University of Warwick culture collection. The isolate was passaged through *Galleria mellonella* L. (Lepidoptera: Pyralidae) larvae by immersing larvae for 10 s in distilled water containing 0.03% polysorbate (Tween®) 80 and 1.5×10^8 colony-forming units (CFU) mL^{-1}. Sporulating cadavers were streaked onto Sabouraud dextrose agar (SDA) plates (90 mm Petri dishes containing 20 mL medium) amended with chloramphenicol (50 μg mL^{-1}) and subsequently subcultured onto fresh SDA plates to obtain pure cultures. Final plates were stored under sterile incubation conditions (Heratherm, Thermo Fisher Scientific inc, Cheshire, UK (25 ± 1°C)) until required. Thirty aphids (third instar) used as infected odour sources were inoculated with the same fungal suspension using a hand-held atomiser. Spores were applied from a standardised distance of 10 cm and treated aphids were then transferred to fresh leaf discs placed in SDA plates.

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Behavioural response to entomopathogenic fungi

Behavioural assays were carried out in a Perspex four-arm olfactometer, similar to that described by Pettersson (1970) and following general good practice for insect olfactory bioassays (Roberts et al., 2023). In the assay testing *B. bassiana* alone, odour sources comprised (i) an agar plug colonised by *B. bassiana*, (ii) a sterile agar plug control and (iii–iv) two blank arms receiving charcoal-filtered air, drawn through the apparatus by a low-pressure vacuum pump at 800 mL min^{-1}. Individual adult apterous aphids were introduced singly into the central arena and allowed to explore the apparatus. The time spent in each odour zone was recorded and subsequently expressed as the proportion of total observation time allocated to each arm. To minimise positional bias, odour sources applied to each arm was changed between replicates, and the olfactometer was cleaned between runs using distilled water and absolute ethanol before air drying in a fume hood for 60 min. Each assay lasted 15 min, with 20 replicates completed.

Behavioural response to infected conspecifics

In the second four-arm olfactometer assay, odour sources comprised (i) conspecific adult aphids previously inoculated with *B. bassiana*, (ii) healthy conspecific adult aphids handled identically but without fungal inoculation, (iii) an agar control and (iv) a blank-air control. Healthy and infected odour-source aphids were maintained under identical environmental conditions prior to assay. Test aphids were assessed individually in the same four-arm olfactometer, and the proportion of time spent in each odour zone was recorded as previously described, with identical airflow, filtration and cleaning procedures. Each assay lasted 15 min, with 70 replicates completed.

Statistical analysis

Time spent in each odour zone was converted to proportional data. Because olfactometer allocations are compositional and constrained to sum to one, proportions were centred log-ratio (CLR) transformed prior to analysis (Aitchison, 1982). For each assay, candidate Gaussian linear mixed models were compared using Akaike information criterion (AIC) and AICc to identify the best-supported model structure. Odour source was included as a fixed effect and olfactometer arm was initially included as a random effect to account for potential positional bias. Post hoc comparisons were carried out using estimated marginal means with Dunn–Šidák adjustment. Analyses were completed in R v4.4.2 (R Core Team, 2024) using the packages compositions (van den Boogaart & Tolosana-Delgado, 2008), lme4 (Bates et al., 2015), emmeans (Lenth & Piaskowski, 2025) and AICcmodavg (Mazerolle, 2023).

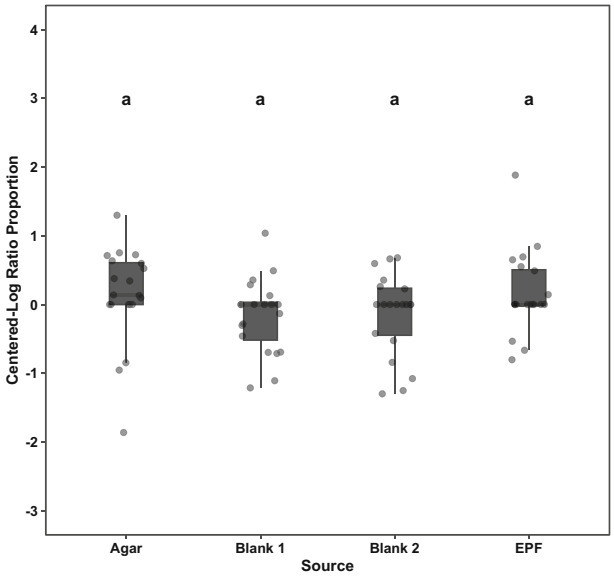


FIGURE 1 Relative arm occupancy of aphids in a four-arm olfactometer when exposed to odours from an agar control (Agar), two blank (charcoal-filtered air) controls (Blank 1 and Blank 2), and EPF-colonised agar (EPF). Values are shown as centred log-ratio (CLR) transformed proportions of aphids in each arm. Grey points represent individual observations; boxplots show the median and interquartile range; whiskers indicate the data range excluding outliers. "ns" indicates no significant differences among odour sources (GLM, $p > 0.05$).

RESULTS

Behavioural response to entomopathogenic fungi

When aphids were exposed to *B. bassiana* alone, behavioural responses did not differ significantly among odour sources (Figure 1). The best-supported model indicated no significant effect of source on the CLR-transformed proportion of time spent in olfactometer zones ($F_{3,76} = 1.59$, $p = 0.198$; AIC = 153.7). In absolute terms, aphids spent a mean (±SE) of 157.9 ± 41.6 s in the arm containing *B. bassiana*-colonised agar, compared with 252.8 ± 50.9 s in the agar control arm, 116.4 ± 25.2 s in blank arm 1 and 140.1 ± 46.0 s in blank arm 2. When calculated within individual trials, these values corresponded to 28.4 ± 7.7%, 36.6 ± 7.3%, 16.5 ± 3.6% and 18.5 ± 5.5% of recorded arm time, respectively. Estimates for the EPF odour did not differ from those for the agar or blank controls, and confidence intervals for all sources overlapped zero. No significant differences were detected among the control treatments.

Behavioural response to infected conspecifics

Behavioural responses differed significantly among odour sources when aphids were exposed to infected conspecifics (Figure 2). Model selection identified odour source as the strongest predictor of aphid spatial preference, with no support for an effect of olfactometer arm or an

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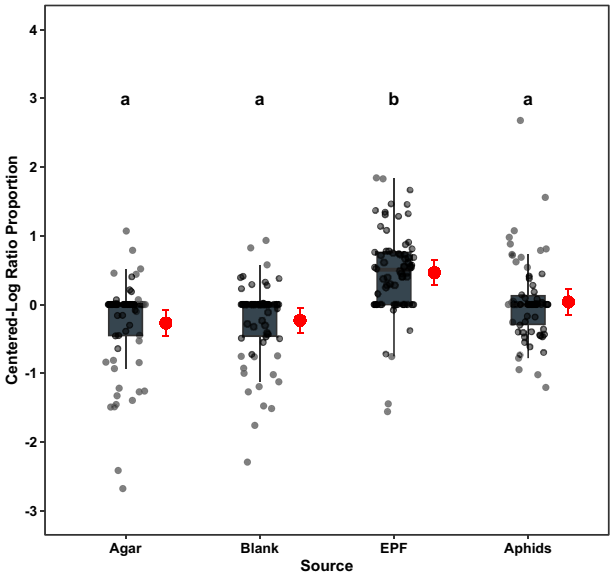


FIGURE 2 Relative arm occupancy of *Myzus persicae* in a four-arm olfactometer when exposed to odours from an agar control (Agar), a blank control (Blank), EPF-infected conspecifics (EPF) and healthy conspecifics (Aphids). Values are shown as centred log-ratio (CLR) transformed proportions of time spent in each arm. Grey points represent individual observations, boxplots show the median and interquartile range, whiskers indicate the data range excluding outliers, and red points with error bars show model-estimated marginal means ± SE. Different letters indicate significant differences among odour sources based on post hoc pairwise comparisons.

arm × source interaction ($F_{3,276} = 20.84$, $p < 0.001$; AIC = 531.1). There was no evidence that positional effects influenced aphid behaviour. Aphids spent longer in the arm containing EPF-infected conspecifics relative to all other odour sources. In absolute terms, aphids spent a mean (± SE) of 397.5 ± 31.5 s in the arm containing infected conspecifics, compared with 176.6 ± 23.7 s in the arm containing healthy conspecifics, 126.4 ± 24.8 s in the agar control arm and 121.2 ± 20.5 s in the blank-air control arm. When calculated within individual replicates as a proportion of total recorded arm time, these values corresponded to 47.1 ± 3.6%, 21.2 ± 2.8%, 15.4 ± 3.0% and 16.3 ± 3.0%, respectively. Aphids, therefore, spent on 220.9 s longer in the arm containing infected conspecifics than in the arm containing healthy conspecifics and more than 270 s longer than in either control arm. The proportion of time spent in the EPF-infected arm was significantly greater than that in the agar control ($t_{276} = -7.02$, $p < 0.001$), the blank arm ($t_{276} = -6.64$, $p < 0.001$) and the arm containing healthy conspecifics ($t_{276} = 4.07$, $p = 0.0004$). Aphids also responded positively to healthy conspecifics compared to the agar control ($t_{276} = -2.95$, $p = 0.018$), although the magnitude of the response was substantially greater for infected individuals (estimated marginal mean: 0.46 ± 0.07) than for healthy ones (0.04 ± 0.07).

DISCUSSION

This study demonstrates that behavioural responses of *M. persicae* to EPF-associated odours are strongly context dependent. Aphids did not discriminate between *B. bassiana*-colonised agar and the control treatments, yet they responded positively to odours associated with conspecifics infected by the same fungus. This contrast indicates that cues associated with fungal odours may only have behavioural modifying chemicals when associated with host infection.

The absence of a recordable response of *M. persicae* to *B. bassiana* grown on agar differs from the positive responses previously reported for this aphid species to *B. bassiana* mycelia and conidia (Geedi et al., 2023). However, this difference is not necessarily contradictory. EPF emit complex and dynamic volatile blends, the composition of which depends on strain, culture substrate, nutritional status and growth stage (Bojke et al., 2018; Holighaus & Rohlfs, 2016). Behavioural outcomes may also be influenced by assay configuration and the physiological state of the responding insect (Roberts et al., 2023). The data presented here, therefore, do not suggest that *M. persicae* is universally insensitive to *B. bassiana* volatiles; rather, they indicate that the odour profile produced by colonised agar in this experiment was not sufficient to elicit a behavioural response in test aphids. The positive response of aphids to infected conspecifics warrants closer consideration. Infection is likely to modify the odour environment through fungal VOCs produced on or within the host, and through infection-mediated changes in host metabolism, cuticular chemistry or excreted semiochemicals (Butt et al., 2016). Pathogens can profoundly alter insect chemical communication, at times suppressing defence signals and at others exploiting host odours to enhance their own transmission (Moyano et al., 2023; Naundrup et al., 2022; Zhang et al., 2024). Our findings are consistent with the hypothesis that *B. bassiana* infection generates a distinctive composite odour blend that results in healthy aphids spending longer in the presence of this stimulus. Aphid alarm-pheromone biology may be relevant to this process.

From both ecological and applied perspectives, attraction or arrestant behavioural responses to infected aphids could increase local contact rates between susceptible hosts and infectious propagules, thereby influencing horizontal transmission. This is consistent with previous work showing that aphid foraging behaviour can expose individuals to entomopathogens and that infected aphids do not necessarily avoid sites where transmission risk is elevated (Baverstock et al., 2005). More broadly, the effects of EPF on aphid behaviour extend beyond direct infection. Endophytic colonisation of plants by EPF can alter plant volatile emissions and aphid preference, sometimes attracting aphids even when subsequent performance is reduced (Fingu-Mabola et al., 2020, 2021; Wilberts et al., 2022). These studies suggest that EPF may influence aphid movement and population processes through multiple odour-mediated pathways.

Future studies should determine the chemical basis and temporal dynamics of the behavioural responses reported here. Headspace analysis of healthy and infected aphids, coupled with electrophysiology and behavioural bioassays, would help to distinguish fungal metabolites from host-derived cues. It will also be important to test how host plant species, aphid instar and morph, infection stage and sporulation status shape the emitted signal because these factors are likely to influence both odour production and behavioural

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interpretation (Pickett et al., 1992; Roberts et al., 2023; Webster, 2012). *Myzus persicae* did not respond detectably to *B. bassiana* grown on agar but responded strongly to odours from infected conspecifics, identifying a previously underappreciated dimension of aphid–EPF interactions with clear relevance to aphid chemical ecology and biological control.

AUTHOR CONTRIBUTIONS

Ben J. Clunie: Conceptualisation; methodology; formal analysis; data curation; visualisation; project administration; writing—original draft; writing—review and editing. **Thomas Bluck**: Investigation; data curation. **Imogen Crowe**: Investigation; data curation. **Devan Coyne**: Investigation; data curation. **Aidan Smith**: Investigation; data curation. **Tom W. Pope**: Conceptualisation; methodology; supervision, writing—review and editing. **Joe M. Roberts**: Conceptualisation; methodology; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known financial or non-financial conflicts of interest that could have appeared to influence the work reported in this paper. There are no disputes regarding the ownership of the data presented, and all contributions have been appropriately attributed through co-authorship and acknowledgements.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://figshare.com/account/articles/31833445, reference number https://doi.org/10.6084/m9.figshare.31833445. Clunie et al, 2026.

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